ZOOLOGICAL SCIENCE 7: 29–38 (1990)

A Comparative Study of the Gill Morphometry in the Mudskippers-*Periophthalmus chrysospilos, Boleophthalmus boddaerti* and *Periophthalmodon schlosseri*

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ABSTRACT—The gill and skin morphometries of three mudskippers-*Periophthalmus chrysospilos, Boleophthalmus boddaerti* and *Periophthalmodon schlosseri* were studied and compared. Correlations were made between the morphometric parameters of these respiratory surfaces and the different terrestrial and aquatic affinities of the mudskippers with special reference to their capabilities to respire terrestrially.

The natural preference of *B. boddaerti* for an aquatic environment can be explained by their having the longest and greatest number of gill filaments amongst the three mudskippers studied. It also has the largest gill area and gill area: skin area ratio, indicating a greater role of its gills than its skin in respiration.

Both *P. chrysospilos* and *P. schlosseri* have relatively lesser affinity to water as their gills are not well adapted for aquatic respiration. *P. chrysospilos* has the smallest total number of filaments and shortest total filament length. It also has smaller gill area: skin ratio than *B. boddaerti,* and exhibits the most rapid increase in skin area with respect to body weight. Thus, its skin appears to have a greater role in gaseous exchange than its gills. In *P. schlosseri,* the gill area : skin area ratio increases as the fish grows, suggesting that small fish depends more on its skin for gaseous exchange whilst branchial respiration is more important in bigger individuals.

INTRODUCTION

Much of the information available on air-breathing fish generally deals with their diverse respiratory adaptations to their mode of life. Accessory breathing organs of air-breathing fish eg. *Channa, Saccobranchus, Clarias, Anabas* [1] and *Heteropneustes fossilis* [2] have been examined and described. The various respiratory areas of air-breathing fish have also been measured [1, 3]. In general, the gill area in air-breathing fish is smaller than non air-breathing aquatic fish. Even air-breathing fish which never leave water have relatively small gill area [4, 5].

Much interest has also been centered on amphibious fishes, mainly the mudskippers. Mudskippers are unique in being some of the most terrestrial fishes [6]. Hence, most of the information collected on mudskippers had placed major emphasis on their physiological [7–10] and biochemical [11–15] adaptations to terrestrial exposure.

The three major genera of mudskippers in Singapore are *Periophthalmus chrysospilos, Boleophthalmus boddaerti* and *Periophthalmodon schlosseri.* They live in the same vicinity at Pasir Ris estuary, off the east coast of Singapore, but differ markedly in behavior and microhabitat. *B. boddaerti* and *P. schlosseri* are found on the intertidal zone of the mudflats whereas *P. chrysospilos* inhabits the littoral zone of the seashore nearby. Of the three mudskippers, *B. boddaerti* has the greatest affinity for water. At low tide, it is found on the mudflats and it periodically enters the water. But, as the tide rises, it retreats into its burrows which are on the lower region of the mudflats and remains submerged until the tide ebbs. *P. schlosseri* and *P. chrysospilos* have less affinity for water compared to *B. boddaerti.* At low tide, *P. schlosseri* comes onto the mudflats; at

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Accepted February 20, 1989
Received October 11, 1988

high tide, they are usually found swimming along the water's edge with their snout above water. *P. chrysospilos* is almost invariably found on land next to water at both high and low tides. When agitated, *B. boddaerti* dives and remains submerged for some time whereas *P. schlosseri* and *P. chrysospilos* skim away at the water surface through several bounces. Low *et al.* [16] studied the gill morphologies of these three genera of mudskippers in Singapore by scanning electron microscopy and reported their structural adaptations to be very different.

One of the problems mudskippers face upon terrestrial exposure is that their gills may collapse and their secondary lamellae tend to coalesce, resulting in a major reduction in functional respiratory area available for gaseous and ionic exchange. The gill morphometry of the mudskippers *B. boddaerti* [17, 18], *B. chinensis* and *P. cantonensis* [19] have been studied. Although the gill morphometry of *B. boddaerti* from the Arabian Gulf has been studied by Hughes and Al-Kadhomiy [18], the behavior reported in their investigation was very different from that observed in our local species. In contrast to the local *B. boddaerti*, the specimens studied by Hughes and Al-Kadhomiy [18] were found at the water's edge during high tide. Moreover, the local mudskipper is herbivorous [20] whereas the Arabian Gulf *B. boddaerti* is reported to be omnivorous. Since no detailed information on the gills of *P. schlosseri* is available and the most recent report on those of *P. chrysospilos* concerned more about the gill morphology than morphometry [16], the presence of the three local mudskippers in Pasir Ris therefore presented the authors with a unique opportunity to compare their gill morphometries and skin areas in relation to body sizes and their variable capabilities to respire terrestrially. It is hoped that this study can explain the very different behavioral strategies of these mudskippers in their natural habitats.

MATERIALS AND METHODS

Mudskippers ranging from young to fully grown adults, (2 to 13 g for *P. chrysospilos*, 2 to 35 g for *B. boddaerti* and 3 to 111 g for *P. schlosseri*) were captured from August to September in 1986, at Pasir Ris, Singapore. These mudskippers were identified according to Khoo [20]. Normal breeding period of the mudskippers in Singapore was observed to be between May and July. No measurement was made on gravid specimens and no attempt was made to separate the sexes. They were maintained in the laboratory in 50% seawater (18‰ salinity). Fish were killed by pithing, lightly blotted dry and their weights recorded by a Shimadzu Libror EB 280M electronic animal balance to the nearest milligram.

Skin morphometry

The skin area was obtained by rolling one side of the mudskipper flat onto a piece of paper and tracing its outline. This outline was retraced onto a piece of paper of even thickness, cut out, and its area determined. This value was doubled to obtain the bilateral skin area of the specimen.

Gill morphometry

Dissected gills were rinsed with 0.85% NaCl solution and immersed in 5% formalin made with 50% sea water. Measurements were made on all four right gill arches. Exposure of the gills to formalin for various periods of time might cause artificial changes to some of the morphometric parameters measured, especially the secondary lamellar area. Therefore, attempt was made to standardise the period of exposure of all the gill samples to formalin before measurement of a specific gill parameter was made. Such procedure ensured that comparison of the specific gill parameters between specimens was valid. The total number of filaments were counted after preservation for one day. On the second day, the total filament length was measured, whilst the number of secondary lamellae/mm and lamellar area were obtained on the third and fourth day respectively.

The method of filament sampling was according to Hughes [21]. The gill parameters were obtained from measurements of every fifth filament in *P. chrysospilos* and *B. boddaerti.* In *P. schlosseri,* however, a substantial number of branched filaments occurred at the centre of the arch [16]. If measurements of the filament length were made on every fifth filament, some of them being branched and others not, it would give rise to a considerable amount of error. Therefore, measurements of filament length were made on every filament on all four right arches in this mudskipper. To measure the number of secondary lamellae/mm, two counts were made near the base and tip of the unbranched or branched filaments. This was performed on every other filament on all four arches. These values were averaged and doubled as there were secondary lamellae on both sides of the filament. They were next multiplied by the total filament length of that gill arch to obtain the number of secondary lamellae.

To determine the secondary lamellar area, the arches of all three species were stained with methylene blue. Four lamellae were excised from the base, four from the tip and four from the middle of the filaments. These were mounted on glass slides. Their outlines were traced by a WILD camera lucida onto even thickness paper which was cut, and the average bilateral areas calculated. This was performed on every fifth filament of *P. chrysospilos* and *B. boddaerti* from which the filament length was obtained. For *P. schlosseri,* three filaments were chosen for this determination-one from the centre (usually branched), and two from the mid-point between the centre and the dorsal and ventral aspects of the arch. The averaged bilateral lamellar area was then multiplied by the number of secondary lamellae to give the gill area of that particular arch. This value was next doubled to account for the left arch as well. The total gill area was obtained by summimg the gill area of all the gill arches.

RESULTS

The results of the skin and gill parameters fit the logarithmic equation:

$$\text{Log } Y = \log a + b \log W$$

or

$$Y = aW^{b}$$

where Y is the parameter measured; W=weight of the fish; a=intercept on the Y axis giving the parameter for a 1 g fish; b=regression coefficient (slope), with correlation coefficients (r) greater than 0.95 for most of the parameters measured (Table 1). The standard deviations of the Y intercept (S_a) and the slope (S_b), are also given in the same table. Unlike most gill morphometric studies, various dimensions for 1, 10 and 100 g fish and 95% confidence limits are not given as these values can be calculated from the equations in Table 1. Bilogarithmic plots of the skin and various gill parameters against body weight are presented in Figures 1, 2, 3 and 4.

The total filament number and total filament length decrease in the order *B. boddaerti*>*P. schlosseri*>*P. chrysospilos* (Fig. 1, Table 1). From the bilogarithmic plots of secondary lamellae/mm against body weight, it can be seen that the decrease in this parameter is slight in *P. schlosseri* and *B. boddaerti* but marked in *P. chrysospilos* (Fig. 2, Table 1). Although the total number of secondary lamellae (N) decrease in the order *B. boddaerti* >*P. schlosseri*>*P. chrysospilos* (Fig. 2), the slope of increase in this gill parameter with body size is the greatest in *P. schlosseri* (Table 1). The regression coefficient in enlargement of bilateral secondary lamellar area (bl) with body

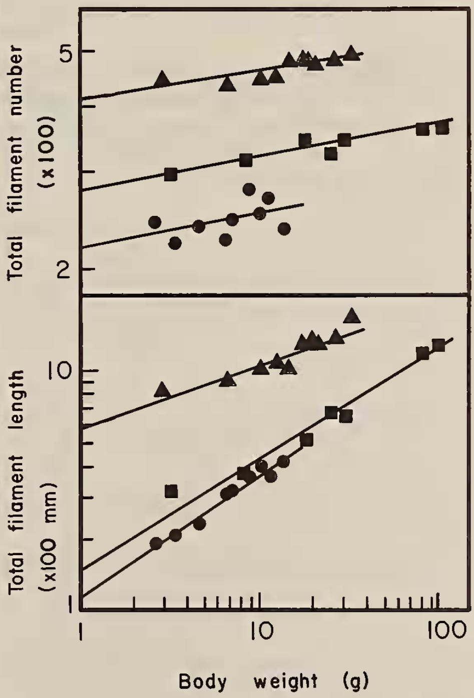

Fig. 1. Bilogarithmic plot of total filament number and total filament length of *P. chrysospilos* (●), *B. boddaerti* (▲) and *P. schlosseri* (■) against body weight.

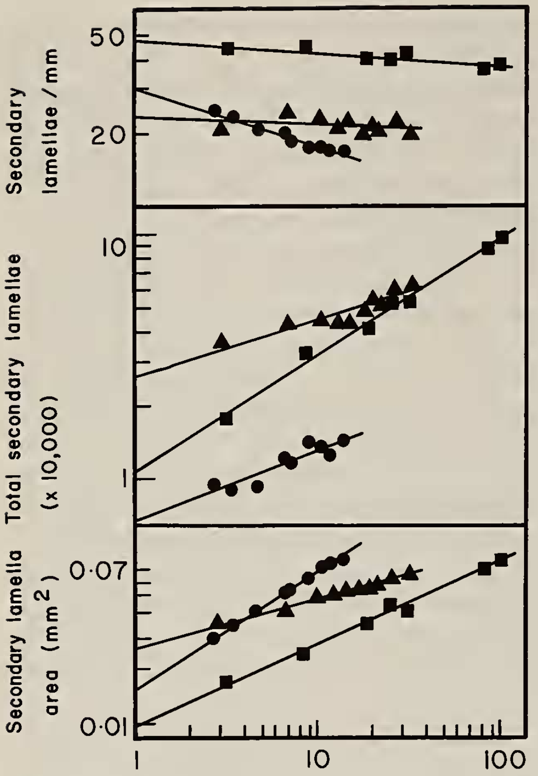

Fig. 2. Bilogarithmic plot of number of secondary lamellae/mm on one side of the filament, total secondary lamellae and average secondary lamella area of *P. chrysospilos* (●), *B. boddaerti* (▲) and *P. schlosseri* (■) against body weight.

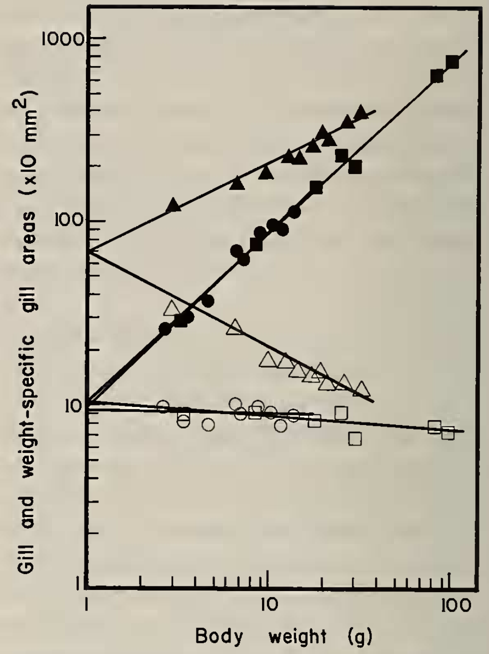

Fig. 3. Bilogarithmic plot of gill area *P. chrysospilos*(●), *B. boddaerti* (▲) and *P. schlosseri* (■) against body weight. Open symbols represent the corresponding weight-specific gill areas of the mudskippers.

Table 1. Summary of equations obtained from regression analysis of the *P. schlosseri*

Parameter	*P. chrysospilos*	S_a	S_b	r
Skin area (mm^2)	Log SA=2.6423+0.8077 log W $SA=439\ W^{0.8077}$	1.0319	0.01582	0.9985
Weight-specific skin area (mm^2/g)	Log S=2.6206−0.1696 log W $S=417\ W^{-0.1696}$	1.0345	0.01712	0.9659
Total number of filaments	Log F=2.3376+0.0629 log W $F=218\ W^{0.0629}$	1.0975	0.04689	0.4517
Total filament length (mm)	Log L=2.0568+0.5033 log W $L=114\ W^{0.5033}$	1.0819	0.03968	0.9788
Number of secondary lamellae/mm (one side)	Log n=1.4802−0.2367 Log W $n=30.2\ W^{-0.2367}$	1.0322	0.01599	0.9844
Total number of secondary lamellae	Log N=3.8209+0.2933 log W $N=6620\ W^{0.2933}$	1.1171	0.05584	0.8933
Average bilateral secondary lamella area (mm^2)	Log bl=−1.8275+0.6456 log W $bl=0.01488\ W^{0.6456}$	1.0211	0.01051	0.9990
Gill area (mm^2)	Log GA=1.9895+0.9577 log W $GA=97.6\ W^{0.9577}$	1.1518	0.07126	0.9813
Weight-specific gill area (mm^2/g)	Log G=1.9679−0.0198 log W $G=92.9\ W^{-0.0198}$	1.1436	0.06765	0.1095

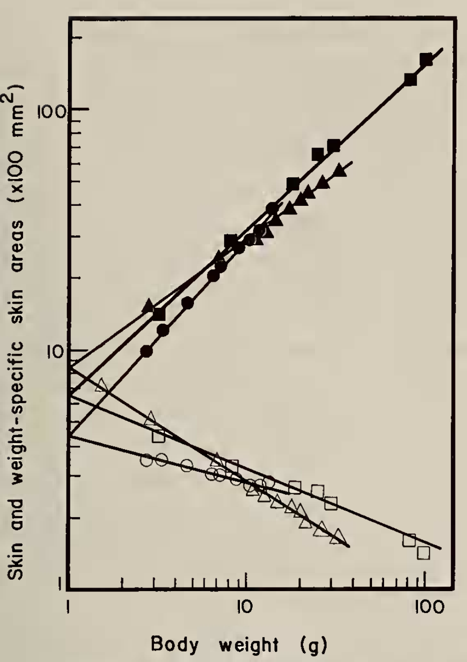

FIG. 4. Bilogarithmic plot of skin area of *P. chrysospilos* (●), *B. boddaerti* (▲) and *P. schlosseri* (■) against body weight. Open symbols represent the corresponding weight-specific skin area of the mudskippers.

weight is smallest in *B. boddaerti* and greatest in *P. chrysospilos* (Fig. 2, Table 1).

B. boddaerti has larger gill area than *P. schlosseri* and *P. chrysospilos* (Fig. 3), but smaller slopes of increase in N and bl with respect to weight. These result in its smallest slope of increase in gill area, and hence its largest slope of decrease in weight-specific gill area with body size among the three mudskippers (Fig. 3, Table 1). In contrast, *P. chrysospilos* and *P. schlosseri* have regression coefficients of increase in gill area with body weight approaching 1, indicating only slight change in weight-specific gill area as the fish grows larger (Fig. 3, Table 1).

The slopes of increase in skin area with body weight increase in the order *B. boddaerti*>*P. schlosseri*>*P. chrysospilos* (Fig. 4, Table 1). Calculated gill area: skin are ratios are plotted against body weight in Figure 5. The ratios for *P. chrysospilos,* which range from 0.27 to 0.36, are smaller than those for *B. boddaerti* (0.67 to 0.77). *P. schlosseri* is unusual in having ratios that increase from 0.22 in small specimens to 0.50 in larger ones (Fig. 5).

A comparison has been made between some gill parameters of the mudskippers with those of various fish species (Table 2) and mudskippers (Table 3) reported elsewhere.

skin areas and the various gill parameters with body weight of *P. chrysospilos, B. boddaerti* and

B. boddaerti	S_a	S_b	r	*P. schlosseri*	S_a	S_b	r
Log SA=2.9250+0.5299 log W SA=841 $W^{0.5299}$	1.0197	0.00753	0.9990	Log SA=2.8015+0.6889 log W SA=633 $W^{0.6889}$	1.0559	0.01627	0.9985
Log S=2.9252−0.4701 log W S=842 $W^{-0.4701}$	1.0197	0.00754	0.9990	Log S=2.8015−0.3112 log W S=633 $W^{-0.3112}$	1.0559	0.01626	0.9920
Log F=2.6109+0.0521 log W F=408 $W^{0.0521}$	1.0221	0.00843	0.9000	Log F=2.4423+0.0615 log W F=277 $W^{0.0615}$	1.0347	0.01021	0.9247
Log L=2.7553+0.2567 log W L=569 $W^{0.2567}$	1.0614	0.02301	0.9659	Log L=2.1629+0.4600 log W L=146 $W^{0.4600}$	1.0898	0.02570	0.9910
Log n=1.3636−0.0307 log W n=23.1 $W^{-0.0307}$	1.0620	0.02323	0.4025	Log n=1.6803−0.0518 log W n=47.9 $W^{-0.0518}$	1.0506	0.01475	0.8432
Log N=4.4162+0.2290 log W N=26074 $W^{0.2290}$	1.0685	0.02557	0.9482	Log N=4.0289+0.4759 log W N=10687 $W^{0.4759}$	1.0723	0.02088	0.9950
Log bl=−1.6002+0.2650 log W bl=0.02511 $W^{0.2650}$	1.0197	0.00718	0.9970	Log bl=−2.0262+0.4491 bl=0.00942 $W^{0.4491}$	1.0646	0.01870	0.9955
Log GA=2.8319+0.4812 log W GA=679 $W^{0.4812}$	1.1032	0.03618	0.9783	Log GA=2.0012+0.9312 log W GA=100 $W^{0.9312}$	1.1257	0.03539	0.9965
Log G=2.8325−0.5194 log W G=680 $W^{-0.5194}$	1.1029	0.03607	0.9798	Log G=2.0012−0.0688 log W G=100 $W^{-0.0688}$	1.1257	0.03540	0.6557

TABLE 2. Comparison of the computed values of total filament number (F), total filament length (L) and gill area (GA) obtained in the present studies for 10 g mudskippers and various species of fish of equivalent weight reported elsewhere

Fish species at 10 g	F	L (×100 mm)	GA (×1000 mm^2)	Reference
Aquatic fishes				
Cyprinus carpio	1110	23.2	5.17	25
Katsuwonus pelamis	—	137	262	26
Thunnus sp.	—	135	200	26
Air-breathing fishes				
Anabas testudineus	1049	11.2	2.29	1
Channa punctuata	1111	14.9	1.84	3
Mudskippers				
P. chrysospilos	251	3.63	0.89	Present study
B. boddaerti	460	10.28	2.06	Present study
P. schlosseri	547	4.21	0.86	Present study

— value is not available as regression analyses were not performed on this gill parameter

TABLE 3. Comparison of gill measurements of the local mudskippers *P. chrysospilos* (*P. chry.*), *B. boddaerti* (*B. b.*) and *P. schlosseri* (*P. s.*) with the *B. boddaerti* studied by Niva *et al.* (17) and Hughes and Al-Kadhomiy (18). The measurements of 8.8 g *Periophthalmus cantonensis* (*P. can.*) and 53 g *Boleophthalmus chinensis* (*B. c.*) by Tamura and Moriyama (19) are also given

	Tamura & Moriyama		Present study				Niva *et al.*	Hughes & Al-Kadhomiy
Gill measurement	8.8 g *P. can.*	53 g *B. c.*	8.8 g *P. chry.*	8.8 g *P. s.*	53 g *B. b.*	53 g *P. s.*	53 g *B. b.*	53 g *B. b.*
Total filament number	306	486	249	317	502	354	630	—
Total filament length (mm)	495–510	2500–2969	340	396	1577	904	2179	3678
Number of secondary lamellae/mm (one side)	21–26	12–16	18.1	42.8	11.8	39.0	17.7	10.7
Average bilateral secondary lamella area (mm^2)	0.040	0.080	0.061	0.025	0.072	0.056	0.061	0.076
Total secondary lamellae	23617	77532	12529	30085	64723	70706	77975	78870
Gill area (mm^2)	1050–1150	5020–5551	783.5	759.8	4587	4044	4695	5979

DISCUSSION

The amphibious nature of all three genera of mudskippers is undisputable. However, their relative success in terrestrial adaptation and their strategies for terrestrial respiration may be very different. *B. boddaerti* enters and submerges itself in water frequently whereas *P. chrysospilos* and *P. schlosseri* stay on land most of the time. Thus, the mudskippers have marked differences in their dependence on an aquatic environment. Tamura and Moriyama [19] pointed out that a small gill area necessarily leads to a smaller role of branchial respiration. Hence, the relationship between the skin and gill area may explain the behavioral differences in these mudskippers.

P. chrysospilos has a smaller gill area than *B. boddaerti* (Fig. 3) and the fewest and shortest filaments of the three mudskippers (Fig. 1). As its filaments are bent and twisted [16], not all of its secondary lamellae will be oriented parallel to the respiratory water current, making the countercurrent distribution mechanism for oxygen absorption inefficient. Therefore, oxygen uptake in this mudskipper has to be supplemented by other surfaces such as the skin, be it in water or on land. In general, the respiratory medium-blood distance of skin is much thicker than that of gill epithelia. Nevertheless, cutaneous respiration in *P. chrysospilos* could be more efficient in air where the medium is less dense and the diffusion rate of oxygen would be higher as relatively more oxygen is available (200 μl oxygen/ml air compared to 5 μl oxygen/ml water). The importance of cutaneous respiration in *P. chrysospilos* is further reflected in its small gill: skin area ratio (Fig. 5) as compared to *B. boddaerti.* Since cutaneous respiration is important for this mudskipper, it exhibits the greatest slope of increase in skin area and the smallest slope of decrease in weight-specific skin area with respect to weight (Fig. 4, Table 1). The results of Tamura *et al.* (22) are in support of our hypothesis of the importance of cutaneous respiration in this genera of mudskipper. Their studies showed that *P. cantonensis* relies on its skin for 76% and its gills for 27% of its oxygen uptake on land. When confined to water, the oxygen uptake by the skin and gills were about equal (48% and 52% respectively). Thus, for respiratory reasons, *P. chrysospilos* may remain on land most of the time. Furthermore, the gills of *P. chrysospilos* have adaptive features to withstand aerial exposure. Graham [23] suggested that greater spacing between secondary lamellae reduces collapse of the respiratory surfaces in air. Secondary lamellar frequency in *P. chrysospilos* is indeed lower and decreases markedly body weight as compared to the other two mudskippers (Fig. 2, Table 1).

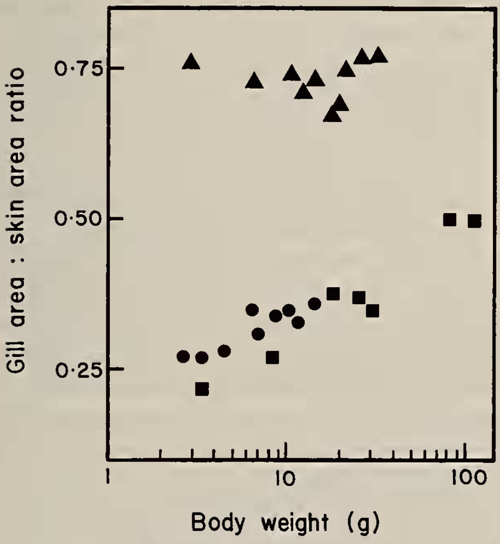

Fig. 5. Plot of gill area: skin area ratio of *P. chrysospilos* (●), *B. boddaerti* (▲) and *P. schlosseri* (■) against logarithmic body weight.

In contrast, *B. boddaerti* has the longest and greatest number of filaments (Fig. 1) of the three mudskippers. Long filaments are more likely to collapse when removed from water. Although *B. boddaerti* of body weights greater than 4 g have smaller secondary lamellar area than *P. chrysospilos* of similar weight (Fig. 2), the former have comparatively greater number of lamellae/mm (Fig. 2). Thus, the secondary lamellae may tend to coalesce upon removal from water. All these factors lead to the reduced preference of *B. boddaerti* for land compared to the other two mudskippers. However, its filaments are more aligned [16], hence, most of the secondary lamellae may be in the optimal position to fully utilise the countercurrent mechanism for aquatic gaseous exchange. Also, since it has the largest gill area (Fig. 3), weight-specific gill area (Fig. 3) and gill area: skin area ratio of the three mudskippers (Fig. 5), its greater affinity for water can be easily appreciated. The results of the present studies are in agreement with those reported by Tamura and Moriyama [19] for *B. chinensis*. Since the gills of *B. boddaerti* are playing a greater role in respiration, therefore measurements reveal that the slope of increase in skin area with respect to weight in this fish is the smallest of the three mudskippers (Table 1, Fig. 4).

The bilogarithmic plots of gill area and weight-specific gill area of *B. boddaerti* against body weight are notably different from those of *P. chrysospilos* and *P. schlosseri*. The gill area of a fish is determined by its total number of secondary lamellae and average secondary lamellar area. As the regression coefficients of the increase in these two gill parameters with body weight in *B. boddaerti* is the smallest of the three mudskippers (Table 1, Fig. 2), it thus results in its smallest slope of increase in total gill area with body weight (Fig. 3, Table 1). A consequence of its small slope of increase in gill area is the rapid reduction in its weight-specific gill area as the fish grows larger (Fig. 3, Table 1). A greater slope of increase in gill area may restrict the terrestrial capability of *B. boddaerti,* for it necessarily result from a greater increase in either total number of secondary lamellae, or average bilateral lamellar area, or both of these gill parameters with body weight. If its regression coefficient of increase in secondary lamellar area with body weight is similar to that of *P. chrysospilos,* its secondary lamellae will be so large that they may fold over removed from water and thus reduce the respiratory area. An increase in the total number of secondary lamellae without a concomitant increase in filament length would lead to a high lamellar frequency. A high lamellar frequency implies closely spaced secondary lamellae which will tend to coalesce upon aerial exposure. If the filament length were to increase to accomodate these secondary lamellae, these longer filaments will have a greater tendency than shorter ones to collapse when the fish emerges from water.

The gills of *P. schlosseri* are not well adapted for aquatic respiration. Low *et al.* [16] reported the presence of intrafilamentary secondary lamellar fusions in the gills of *P. schlosseri.* This may prevent water from flowing between the lamellae and impede oxygen uptake by the counter-current mechanism of the gills. Its total filament length (Fig. 1) and gill area (Fig. 3) are similar to those of *P. chrysospilos. P. schlosseri* is also frequently found out of water in its natural habitat. In addition, the gills of *P. schlosseri* can withstand desiccation as the fenestrae formed by the tissue fusions between secondary lamellae may trap water, reducing the risk of gill dehydration upon terrestrial exposure [16].

Small *P. schlosseri* have smaller gill area: skin area ratio (Fig. 5) as compared to bigger ones. This suggests that small *P. schlosseri,* like *P. chrysospilos,* may have greater dependence on cutaneous than branchial respiration. *P. schlosseri,* on the other hand, can attain a size of greater than 100 g. At 100 g, presumably its skin would be much thicker than those of the other two mudskippers at their respective maximum sizes. Furthermore, the surface area: volume ratio would be smaller in a large fish compared to a small one. Cutaneous respiration in bigger *P. schlosseri* may thus be relatively inefficient. However, it has branched filaments (16) which naturally have more filament tips than unbranched ones. As secondary lamellae are added towards the tip of gill filament, more tips would therefore increase the potential of generating a greater total number of secondary lamellae and, hence, gill area as the fish grows. This potential is clearly shown in its large slopes of increase in total secondary lamellae and gill area with weight (Figs. 2, 3, and Table 1). The gill area: skin area ratio of *P. schlosseri* increases with size from 0.22 until it reaches 0.50 in larger specimens (Fig. 5). This indicates that its gills play a bigger role than its skin in respiration as this mudskipper grows.

Comparison with aquatic fishes, air-breathing fishes and other mudskippers

Schottle [24] and Graham [23] found that air-breathing and amphibious fishes have reduced and length of filaments as well as gill area relative to aquatic fishes. Indeed, these paramenters in the mudskippers are smaller than both aquatic and air-breathing fishes (Table 2). The exception is *B. boddaerti,* which has slightly longer filament length and greater gill area than *Channa punctuata* (Table 2). These air-breathing fishes spend most of their time in water and occasionally surface to breathe whereas mudskippers come on land often. Thus, the fewer and shorter filaments of mudskippers may be correlated to their greater terrestrial capabilities [23].

When similar weight *Periophthalmus* (8.8 g) were compared, it is notable that *P. chrysospilos* has many smaller gill parameters than *P. cantonensis* [19], resulting in a smaller gill area (Table 3). It is possible that the *B. boddaerti* studied by Niva *et al.* [17] and Hughes and Al-Kadhomiy [18] are of a dissimilar species from the local counterpart as they have different observed swimming and feeding behaviors. Most of the gill paramenters of the local species are considerably divergent from those of *B. boddaerti* in previous studies (Table 3), pointing also towards this possibility. No detailed data has been collected on the gill morphometry of *Periophthalmodon.*

P. schlosseri at 8.8 g have comparable total filament length and gill area to *P. chrysospilos* whilst its total filament number approximates that of *P. cantonensis* of similar weight (Table 3). However, *P. schlosseri* has fewer and shorter filaments, and smaller gill area than a similar sized *Boleophthalmus* (Table 3). In addition to its unique gill morphology of branched filaments and intrafilamentary secondary lamellar fusions, *P. schlosseri* has smaller lamellae but higher lamellar frequency than *Periophthalmus* and *Boleophthalmus.*

ACKNOWLEDGMENTS

This study was supported by grants RP 70/85 and RP 860337 from the National University of Singapore.

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